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Differences in demographic traits of four butterflyfish species between two reefs of the Great Barrier Reef separated by 1200 km

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Abstract

Many species demonstrate variation in life history attributes in response to gradients in environmental conditions. For fishes, major drivers of life history variation are changes in temperature and food availability. This study examined large-scale variation in the demography of four species of butterflyfishes (*Chaetodon citrinellus*, *C. lunulatus*, *C. melannotus*, and *C. trifascialis*) between two locations on Australia's Great Barrier Reef (Lizard Island and One Tree Island, separated by approximately 1200km). Variation in age-based demographic parameters was assessed using the re-parameterised von Bertalanffy growth function. All species displayed measurable differences in body size between locations, with individuals achieving a larger adult size at the higher latitude site (One Tree Island) for three of the four species examined. Resources and abundances of the study species were also measured, revealing some significant differences between locations. For example, for *C. trifascialis*, there was no difference in its preferred resource or in abundance between locations, yet it achieved a larger body size at the higher latitude location, suggesting a response to temperature. For some species, resources and abundances did vary between locations, limiting the ability to distinguish between a demographic response to temperature as opposed to a response to food or competition. Future studies of life histories and demographics at large spatial scales will need to consider the potentially confounding roles of temperature, resource usage and availability, and abundance / competition in order to disentangle the effects of these environmental variables.

Introduction

The importance of understanding demographic and life history characters of fish populations has long been recognized, particularly with respect to management of species of economic importance. Increasingly, studies are investigating the intra-specific patterns of variation in life history across geographical scales spanning hundreds or thousands of km, and it is common to find differences in growth rate, body size, and longevity between populations of fish living at different latitudes (e.g., Robertson et al. 2005) and in different ocean basins (e.g., Trip et al. 2008). Regional temperature differences are often considered to play a central role in driving the responses in these traits (e.g., Robertson et al. 2005; Ruttenberg et al. 2005).

Proper understanding of the mechanisms that drive the response of life-history traits across spatial scales is central to effective management. Traits such as growth, age at maturity, and longevity are key parameters in sustainable harvest models. Given the prevalence of geographic variation in these traits, it is prudent to investigate local populations rather than applying a model based on parameters measured in another location. If mechanisms are eventually understood, managers could even begin to anticipate population responses to climate change (Munday et al. 2009). Shifting environmental regimes may subsequently impact a specific population's dynamics, requiring an adaptive management strategy.

Species distributed over large geographic and latitudinal ranges are often exposed to significant variation in environmental conditions, and frequently exhibit geographical differences in life-history traits. In general, ectotherms grow slower but achieve a larger size at higher latitudes (Temperature-Size Rule, Atkinson 1994; Atkinson and Sibly 1997; Kingsolver and Huey 2008). Coral reef fishes exhibit marked variation in life history dynamics among geographically

separated locations and with latitude. In particular, body size and longevity exhibit strong negative relationships with temperature, such that the largest and oldest fishes are typically found in higher latitudes (e.g., Meekan et al. 2001; Robertson et al. 2005; Trip et al. 2008).

In reality, however, temperature is only one of many other variables that may influence life history characters. Density of conspecifics or other competitors (Gust et al. 2002), presence of predators (Stallings 2008), resource availability (Berumen and Pratchett 2008), fishing pressure (Graham et al. 2005), and physical habitat (e.g., exposure, Robertson et al. 2005) are among the many variables capable of influencing various life history and demographic parameters, but these factors may be difficult to control for (or even measure) for most species when conducting large-scale comparisons (e.g. Crossman et al. 2005).

The response of demographic and life history traits to temperature may particularly vary depending on resource availability (Munday et al. 2008; Donelson et al. 2010). The standard hypotheses accompanying temperature-driven variation in life history traits have not, to our knowledge, ever been tested under conditions in which it was possible to control or measure food resource availability at a large scale. Numerous experimental studies show that food quality or availability directly affects growth (Berumen and Pratchett 2008), reproductive lifespan (Lee et al. 2008), reproductive output (Arendt et al. 2005), larval quality (McCormick 2003), and other parameters. It is thus likely that life history traits may be influenced by resources in a way that obscures or amplifies the effects of temperature at a large scale.

The objective of this study was to describe the patterns of demographic variation for four species of butterflyfishes between two geographic locations separated by 1,200 km and 9° of latitude along the Great Barrier Reef, Australia.

Demographic characters that were compared between these populations include initial growth rate, mean maximum adult body size, and mean maximum age (longevity). We predicted that these species would show measureable differences in these life history parameters at this scale. We selected butterflyfish species in which we can easily measure abundance and resource availability, potentially confounding variables that are not typically measured in such studies of coral reef fishes. We are therefore able to examine whether fish abundance and resource availability potentially introduce confounding effects between our sites.

Methods

Study species

The four species examined were *Chaetodon citrinellus, C. lunulatus, C. melannotus,* and *C. trifascialis,* which exhibit distinct prey preferences. *C. citrinellus* is a generalist feeder, consuming prey items from several categories, both coral and non-coral, including small invertebrates and some algal material (Harmelin-Vivien and Bouchon-Navaro 1983; Pratchett 2005). *C. lunulatus* is a hard-coral feeder, but is a "generalist" hard-coral feeder, consuming a very wide range (up to 52 species) of different corals (Pratchett et al. 2004; Berumen et al. 2005; Pratchett 2005). *C. melannotus* is a soft-coral feeder, consuming a variety of coral and non-coral prey, but mostly specializing on soft coral species (Alino et al. 1988; Pratchett 2005). *C trifascialis* is a hard-coral specialist, feeding almost exclusively on just one coral species, *Acropora hyacinthus* (Pratchett 2005). All four species are widespread with geographic ranges encompassing much of the

Pacific Ocean basin (Allen et al. 1998) and are abundant on Australia's Great Barrier Reef (Pratchett and Berumen 2008).

Study location

This study was conducted at two locations in Australia: Lizard Island (14° 40´S, 145° 28´E), located in the northern Great Barrier Reef, and One Tree Island (23° 30´S, 152° 06´E), located in the southern Great Barrier Reef. The two islands are separated by 1,200 km and experience differences in mean annual sea surface temperature (SST) of approximately 2°C (mean annual SST of ~27°C and ~25°C at Lizard Island and One Tree Island, respectively, and mean SST over the summer (January-March) and winter (July-September) months of ~28.7°C and ~24.4°C at Lizard Island, and of ~27.5°C and ~22.5°C at One Tree Island, respectively) (http://www.cdc.noaa.gov, see Trip et al. 2008). At least 29 individuals of the four study species were collected from each reef through 2003 and 2004 (Table 1). Growth rates, densities, and condition of fish may vary among habitats at a given reef (e.g., Gust et al. 2002; Berumen et al. 2005; Pratchett and Berumen 2008), so to avoid these confounding influences, all collections and sampling were undertaken exclusively in haphazardly selected replicate sites on exposed reef crests on the south-east side of One Tree Island and Lizard Island.

Estimation of age

Adults (>50mm TL) were collected by spearing or netting. Juveniles were collected using a clove oil mixture (Munday and Wilson 1997) and hand nets. The total length (TL) of each fish was recorded to the nearest mm; sagittal otoliths

were removed, cleaned and stored dry. Otoliths were prepared following Choat and Axe (1996). Sectioned otoliths were examined using a dissecting microscope (10x) using transmitted light, counting opaque zones. These were presumed to be annular growth increments (Fowler 1995; Berumen 2005). Otoliths that did not display two or more increments were examined using a high-power microscope (400x), and daily increments were counted following Ralston (1976).

Growth modelling and estimation of initial growth rate

Growth was modelled separately for each species from each location using the re-parameterised equation of the von Bertalanffy Growth Function (rVBGF; Francis 1988) (e.g., Welsford and Lyle, 2005; Trip et al. 2008, 2011; Claisse et al. 2009). The rVBGF model parameters express average body size at three arbitrary ages τ, ω and μ, with age ω the average of ages τ and μ. The parameters of the rVBGF equation provide estimates of mean size-at-age at specific ages, thus allowing comparison of mean size-at-age among populations. Ages 1, 3, and 5 were selected so as to best represent the overall form of growth over the majority of each species' life span, from age classes in which size data were well represented. Thus, the parameters used in this study were L_1, L_3 and L_5, with L_1 a measure of mean size-at-age during the growth phase, and L_5 a measure of mean size-at-age during the asymptotic phase of the growth trajectory. Parameters L_1, L_3 and L_5 were estimated by minimising the negative log of the likelihood given a normal probability distribution of size-at-age t (L_t), with mean L_t and standard deviation σ (Haddon 2001). Parameter L_1 was used as an estimate of the average rate of somatic growth experienced between the ages of zero and one year. The percentile

95% confidence intervals (CI) were estimated for each rVBGF parameter using a bootstrapping procedure (Götz et al. 2008).

A Likelihood Ratio Test (LRT) was used to compare growth of each species between One Tree Island and Lizard Island (Kimura 1980; Cerrato 1990; Haddon 2001). The null hypothesis of no difference in growth between locations was rejected at $\alpha = 0.05$, with q degrees of freedom being the difference in the number of parameters constrained under the two hypotheses (e.g., $q = 3$ for coincident curves). LRT allows establishing which growth parameters differ significantly between populations, and therefore whether any differences in growth between populations sampled at the two locations arise from differences in mean size-at-ages one, three, or five years.

Longevity and mean maximum size

Mean maximum age (longevity) and mean maximum size were calculated as the average age (years) and average size (TL, mm) of the 25% oldest individuals of each sample, respectively (Choat and Robertson 2002). A bootstrapping technique was used to estimate 95% CIs around each parameter (longevity and mean maximum size). Original sample means were bias-adjusted, and percentile CIs were calculated from the sorted bootstrapped estimates (Götz et al. 2008). Comparison of 95% CIs provides more conservative results relative to standard significance testing methods (Schenker and Gentleman 2001).

Resource availability

To quantify the availability of coral and non-coral resources that are primarily targeted by the four study species, the abundance (percent cover) and composition of benthic communities were quantified using replicate 50m random-point transects (English et al. 1997). Resource availability was measured using the same transects deployed to assess butterflyfish abundance, giving a total of fifteen transects across three replicate sites at each reef. Corals underlying each of 100 points along each transect were identified to genus; *Acropora* corals were subdivided into morphological categories. All other benthic taxa were categorized to family. Variation in total coral abundance (arcsine transformed) among locations was analysed using one-way ANOVA for key major benthic categories (*Acropora hyacinthus*, other *Acropora* spp., *Montipora* spp., *Porites* spp., other hard corals, soft corals, and non-coral substrate) using R (R Development Core Team 2011).

Butterflyfish density

The majority of competitive interactions involving *C. citrinellus*, *C. lunulatus*, and *C. trifascialis* occur amongst individuals of the same species or with individuals of another of our study species, while non-butterflyfish aggressors are comparatively uncommon (see Table 1 in Berumen and Pratchett 2006). *C. melannotus* is rarely involved in inter-specific competitive interactions (Berumen, pers. obs.). Previous work has shown that where butterflyfishes densities are higher, aggressive interactions are more frequent (Berumen et al. 2005; Berumen & Pratchett 2006). These interactions may restrict access to preferred food resources with flow-on effects to growth or other life history characteristics.

Consequently, mean density was estimated for *C. citrinellus*, *C. lunulatus*, *C. trifascialis* and *C. melannotus* at each location using 50m x 4m visual belt transects, with five replicate transects at each of three sites on the exposed reef crest.

Variation in total density among locations was analysed using ANOVA, while variation in the relative density of species was analysed using multivariate analyses of variance (MANOVA). Univariate homogeneity was tested using Cochran's test and residual plots were examined to confirm MANOVA assumptions of multivariate homogeneity and normality. Pillai's Trace statistic was used to determine the significance of MANOVA results, following Olsen (1976), using SPSS® 16.0.

Results

Size-at-age, growth rate and adult body size

A total of 506 fish were collected and aged for analysis of growth (Table 1). For *C. citrinellus*, *C. lunulatus* and *C. trifascialis*, the relationship between size and age showed an asymptotic form of growth, suggesting fast initial growth, with individuals achieving 68 – 92% of mean maximum (adult) body size by the age of one year. In contrast, *C. melannotus* displayed a comparatively more continuous form of growth, with individuals achieving 36 – 57% of adult size in the first year (Fig. 1).

No significant differences in mean size-at-age one (L_1) were found between Lizard Island and One Tree Island for *C. citrinellus*, *C. lunulatus*, and *C. trifascialis*, suggesting no differences in mean growth rate through the first year of life between locations (Fig. 2, Table 2). In contrast, *C. melannotus* displayed significantly greater mean size-at-age one at One Tree Island (L_1 = 75.1 mm TL) than at Lizard Island (L_1 = 60.2 mm TL) indicating significantly faster growth between the ages of zero and one year at One Tree Island (Fig. 2, Table 2).

Likelihood Ratio Tests indicated significant differences in growth between Lizard Island and One Tree Island for all four species (Table 2). Differences in growth trajectories between locations were explained by differences in expected mean size-at-ages three (L_3) and /or five (L_5). For *C. citrinellus* and *C. trifascialis*, fish were significantly larger from One Tree Island than from Lizard Island by the age of three (Fig. 2, Table 2). For *C. citrinellus*, *C. lunulatus*, and *C. trifascialis*, fish were significantly larger at the age of five years from One Tree Island (Fig. 2, Table 2). In contrast, *C. melannotus* showed no significant differences in expected mean size-at-ages three or five between the two locations sampled (Fig. 2, Table 2). Comparison of mean body size of the 25% oldest individuals sampled confirmed significantly larger adult body sizes at One Tree Island for all species except *C. melannotus*, for which there was no difference in mean maximum size between the two locations (Fig. 3). These results further suggest that estimates of mean size-at-age provided from the rVBGF parameters are reliable estimates to examine differences in adult body size across populations.

Longevity

Examination of mean maximum age (longevity) showed that *C. citrinellus* had a significantly greater mean maximum age at One Tree Island (6.07 – 9.57 years, 95% CI) than at Lizard Island (3.71 – 5.94 years). In contrast, the other three species all showed a greater mean maximum age at Lizard Island than at One Tree Island although those differences were not significant (Fig. 3).

Benthic communities and resource availability

Several categories of benthic cover that represent key food resources for the four study species differed significantly between Lizard Island and One Tree Island (Fig. 4a). *Acropora* spp. (excluding *A. hyacinthus*) (ANOVA, $F_{1,25}$=37.782, P < 0.001), , *Montipora* spp. (ANOVA, $F_{1,25}$=41.431, P < 0.001), and other hard corals (ANOVA, $F_{1,25}$=12.359, P = 0.002) were more abundant at One Tree Island, while soft corals (ANOVA, $F_{1,25}$=6.926, P = 0.014) and all non-coral prey (ANOVA, $F_{1,25}$=34.041, P < 0.001) were more abundant at Lizard Island (Fig. 4a). Abundance of *Acropora hyacinthus* (ANOVA, $F_{1,25}$=0.875, P = 0.359), *Pocillopora* spp. (ANOVA, $F_{1,25}$=0.656, P = 0.426), and *Porites* spp. (ANOVA, $F_{1,25}$<0.001, P = 0.991) did not differ between locations (Fig. 4a).

Butterflyfish density

A total of 406 fish from 23 species were recorded in our density surveys. Mean density of butterflyfishes (presented hereafter as mean no. individuals per 200m^2 ± S.E.) was significantly higher (ANOVA, $F_{1,25}$=5.848, P = 0.023) at One Tree Island (14.4 ± 1.6) compared to Lizard Island (12.6 ± 1.4). The relative density of

our study species and other key chaetodontid species also differed between Lizard Island and One Tree Island (MANOVA, Pillai's trace=0.782, $F_{8,18}$=8.07, P<0.001), however, only *C. lunulatus* exhibited significant differences in density on the exposed reef crest between locations (Fig. 4b). Mean densities of *C. citrinellus, C. melannotus,* and *C. trifascialis* did not differ significantly between locations (Fig. 4b).

Discussion

This study examined the life history traits (initial growth rate, mean maximum adult body size, and longevity) of four butterflyfish species at two locations on Australia's Great Barrier Reef. The four species primarily conformed to predictions of how life history traits may differ between locations with varying temperature regimes. Butterflyfishes from One Tree Island generally grew larger than conspecifics from Lizard Island, a pattern coinciding with that seen in many ectotherms and fishes in response to temperature over gradients of latitude (Temperature-Size Rule or "Hotter is smaller" hypothesis; Kingsolver and Huey 2008). One species, *C. citrinellus* (a generalist feeder), also showed a significant difference in longevity, living longer at the higher latitude location (One Tree Island). Larger body size coupled with greater life span at higher latitudes coincides with the pattern documented for an increasing number of coral reef fishes (e.g., Robertson et al. 2005; Ruttenberg et al. 2005; Trip et al. 2008).

In addition to finding some differences in life history traits, we found notable differences in food resources and congeneric abundances. These types of environmental variables have the capability to influence growth rates (e.g.,

conspecific or competitor density, Gust et al. 2002; resource quality, Berumen and Pratchett 2008). The response seen in the four butterflyfish species examined in this study, however, clearly argues for a role of temperature in shaping large-scale patterns of variation in growth rate, body size, and longevity. In particular, *Chaetodon trifascialis*, among the most specialist of all butterflyfish species (Berumen and Pratchett 2008), almost exclusively consumes the tabular coral *Acropora hyacinthus*. We found no difference in availability of *A. hyacinthus* between One Tree Island and Lizard Island and also found no difference in conspecific abundance between the two sites. Despite this lack of difference in resources or conspecific abundance, we found differences in the mean maximum body size and growth rate (specifically, mean body size at the ages of three, L_3, and five years, L_5) of *C. trifascialis*, with individuals reaching larger body size at One Tree Island, a pattern that coincides with the predicted effect of temperature on body size in the majority of ectotherms (Kingsolver and Huey 2008).

Furthermore, *C. melannotus* grew faster at the higher latitude location (One Tree Island) in the early years of the life span (at the age of one year), even though the preferred resource of *C. melannotus* (soft corals) were significantly more abundant at Lizard Island. If growth rate responded primarily to differences in food availability, we would have expected to find faster growth rates and larger adult body sizes at Lizard Island, a response which is found in conditions of increased food availability (Berrigan and Charnov 1994). In contrast, *C. melannotus* exhibited a higher initial growth rate at the location with comparatively lower abundance of preferred foods (One Tree Island). Work by Conover and colleagues using the Atlantic silverside *Menidia menidia*, has demonstrated that faster growth rates at higher latitudes are correlated with a decrease in temperature (shorter growing season) in species with strong juvenile

mortality rates (countergradient variation model, Conover and Present 1990). The response seen in *C. melannotus* suggests that, in this case, the effect of latitude (temperature) is likely to play a comparatively greater impact on determining initial growth rate than the abundance of food resources.

However, as temperature increases, most organisms experience increased metabolic demands (per unit of body size) (Brown et al. 2004) and greater requirements for food (Munday et al. 2008), and the response of demographic traits to temperature varies with levels of food abundance (Munday et al. 2008; Donelson et al. 2010). Food availability and / or quality is therefore likely to interact intimately with the effects of temperature on the response of life history traits over broad geographic scales. In natural populations, quantifying the relative contributions of temperature and food to the response of life history traits over gradients of latitude is a challenging task, and requires addressing the patterns of variation in diet composition as well as nutrient utilisation and assimilation processes over similar gradients of latitude. At a minimum, researchers need to be aware that food and competition for food could potentially confound or mask findings at these scales. Elucidating underlying mechanisms will not be possible until such data are available. Butterflyfishes are an ideal group to use for studies that seek to incorporate resource usage with environmental variables and other biological/ecological traits due to the ease of surveying the respective communities of fishes, resource usage, and benthic resources used by these species. We acknowledge that the present study falls short of this ambitious goal, but nonetheless it represents a useful starting point for future work seeking to explore the underlying general mechanisms structuring life history characters over geographic scales. Environmental variables such as resource availability and congeneric abundances species are going to be difficult to control for when

sampling at scales as large as common geographic comparisons, but future work establishing life history traits and, particularly, similar studies making large-scale geographic comparisons should endeavour to quantify them, and aim at establishing their relative contributions.

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Reference list

Alino PM, Sammarco PW, Coll JC (1988) Studies of the feeding preferences of *Chaetodon melannotus* (Pisces) for soft corals (Coelenterata; Octocorallia). Proc 6th Int Coral Reef Symp 1:31-36

Allen GR, Steene R, Allen M (1998) A guide to angelfishes and butterflyfishes. Odyssey Publishing, Perth

Arendt KE, Jónasdóttir SH, Hansen PJ, Gärtner S (2005) Effects of dietary fatty acids on the reproductive success of the calanoid copepod *Temora longicornis*. Mar Biol 146:513-530

Atkinson D (1994) Temperature and organism size - a biological law for ectotherms? Adv Ecol Res 25:1-58

Atkinson D, Sibly RM (1997) Why are organisms usually bigger in colder environments-making sense of a life history puzzle. Trends Ecol Evol 12:235-239

Berumen ML (2005) The importance of juveniles in modelling growth: butterflyfish at Lizard Island. Environ Biol Fishes 72:409-413

Berumen ML, Pratchett MS (2006) Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae). Proc 10th Int Coral Reef Symp 1:644-650

Berumen ML, Pratchett MS (2008) Trade-offs associated with dietary specialization for corallivorous butterflyfishes (Chaetodontidae: *Chaetodon*). Behav Ecol Sociobiol 62:989-994

Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). Mar Ecol Prog Ser 287:217-227

Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. Oikos 70:474-478

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85: 1771-1789

Cerrato RM (1990) Interpretable statistical tests for growth comparisons using parameters in the Von Bertalanffy equation. Can J Fish Aquat Sci 47:1416-1426

Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes: an analysis of otolith increments. Mar Ecol Prog Ser 134:15-26

Choat JH, Robertson DR (2002) Age-based studies on coral reef fishes. In: Sale PF (ed) Coral reef fishes, dynamics and diversity in a complex ecosystem. Academic Press, New York, pp 57-80

Claisse JT, Kienzle M, Bushnell ME, Shafer DJ, Parrish JD (2009) Habitat- and sex-specific life history patterns of yellow tang *Zebrasoma flavescens* in Hawaii, USA. Mar Ecol Prog Ser 389:245-255

Conover DO, Present TMC (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83:316–324

Crossman DJ, Choat JH, Clements KD (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. Mar Ecol Prog Ser 296:129-142

Donelson JM, Munday PL, McCormick MI, Pankhurst NW, Pankhurst PM (2010) Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. Mar Ecol Prog Ser 401: 233-243

English S, Wilkinson C, Baker V (1997) Survey manual for tropical marine resources (2nd edn.). Australian Institute of Marine Sciences, Townsville, Australia

Fowler AJ (1995) Annulus formation in the otoliths of coral reef fish: a review. In: Secor DH, Dean JM, Campana SE (eds) Recent developments in fish otolith research. University of South Carolina Press, Columbia, pp 45-63

Francis RICC (1988) Maximum likelihood estimation of growth and growth variability from tagging data. N Z J Mar Freshw Res 22:42-51

Götz A, Kerwath SE, Attwood CG, Sauer WHH (2008) Effects of fishing on population structure and life history of roman *Chrysoblephus laticeps* (Sparidae). Mar Ecol Prog Ser 362: 245-259

Graham NAJ, Dulvy NK, Jennings S, Polunin NVC (2005) Size-spectra as indicators of the effects of fishing on coral reefs fish assemblages. Coral Reefs 24:118-124

Gust N, Choat JH, Ackerman JL (2002) Demographic plasticity in tropical reef fishes. Mar Biol 140:1039-1051

Haddon M (2001) Modelling and quantitative methods in fisheries, Chapman & Hall / CRC, Boca Raton

Harmelin-Vivien ML, Bouchon-Navaro Y (1983) Feeding diets and significance of coral feeding among Chaetodontid fishes in Moorea (French Polynesia). Coral Reefs 2:119-127

Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. Fish Bull 77:765-776

Kingsolver JG, Huey RB (2008) Size, temperature, and fitness: three rules. Evol Ecol Res 10:251-268

Lee KP, Simpson SJ, Clissold FJ, Brooks R, Ballard JWO, Taylor PW, Soran N, Raubenheimer D (2008) Lifespan and reproduction in *Drosophila*: New insights from nutritional geometry. Proc Nat Acad Sci USA 105:2498-2503

McCormick MI (2003) Consumption of coral propagules after mass spawning enhances larval quality of a damselfish through maternal effects. Oecologia 136:37-45

Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. Mar Ecol Prog Ser 212:223-232

Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. J Fish Biol 51:931-938

Munday PL, Kingsford MJ, O'Callaghan M, Donelson JM (2008) Elevated temperature restricts growth potential of the coral reef fish *Acanthochromis polyacanthus*. Coral Reefs 27:927-931

Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. Coral Reefs 28:379-395

Olsen CL (1976) On choosing a test statistic in multivariate analysis of variance. Psychol Bull 83:579-586

Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Mar Biol 148:373-382

Pratchett MS, Berumen ML (2008) Inter-specific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). J Fish Biol 73:1730-1747

Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23:352-356

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org/

Ralston S (1976) Age determination of a tropical reef butterflyfish utilizing daily growth rings of otiliths. US Fish Bull 74:990-994

Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. Mar Ecol Prog Ser 295:229-244

Ruttenberg BI, Haupt AJ, Chiriboga AI, Warner RR (2005) Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia 145:394-403

Schenker N, Gentleman JF (2001) On judging the significance of differences by

examining the overlap between confidence intervals. Am Stat 55: 182-186

Stallings CD (2008) Indirect effects of an exploited predator on recruitment of coral-reef fishes. Ecology 89:2090-2095

Trip EL, Choat JH, Wilson DT, Robertson DR (2008) An inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. Mar Ecol Prog Ser 373:97-109

Trip EDL, Raubenheimer D, Clements KD, Choat JH (2011) Reproductive demography of a temperate protogynous and herbivorous fish, *Odax pullus* (Labridae, Odacini). Mar Freshw Res 62: 176-186

Welsford DC, Lyle JM (2005) Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*). Fish Bull 103:697-711

Figure captions

Figure 1. *Chaetodon* spp. Relationship between size and age of *C. citrinellus*, *C. lunulatus*, *C. melannotus* and *C. trifascialis* at Lizard Island and One Tree Island on the Great Barrier Reef (Australia). The best-fit re-parameterised VBGF (rVBGF) growth model is shown for each species at the two locations. Circles and solid line represent size-at-age data and growth trajectory at Lizard Island, and grey triangles and dashed line represent size-at-age data and growth trajectory at One Tree Island.

Figure 2. *Chaetodon* spp. Comparison of expected mean size-at-ages one, three, and five years in *C. citrinellus*, *C. lunulatus*, *C. melannotus* and *C. trifascialis* between Lizard Island (open bars) and One Tree Island (grey bars) on the Great Barrier Reef (Australia). Re-parameterised von Bertalanffy Growth Function (rVBGF) parameters L_1, L_3 and L_5 are presented with 95% confidence intervals. Likelihood Ratio Test of significant difference in rVBGF parameter values between the two locations is indicated (see Table 2): *** = P < .001 ; ** = P < .01 ; * = P < .05 ; n.s. = not significant (P > .05).

Figure 3. *Chaetodon* spp. Correlation plots of mean maximum size against mean maximum age comparing adult size and longevity of *C. citrinellus*, *C. lunulatus*, *C. melannotus* and *C. trifascialis* between Lizard Island (circles) and One Tree Island (triangles). Means are estimated from the 25% oldest individuals for each population sampled, and are bias-adjusted. Confidence intervals (CI) are 95% percentile CIs estimated from bootstrap estimates.

Figure 4. (a) Mean percent cover of preferred prey resources and (b) mean density of *C. citrinellus*, *C. lunulatus*, *C. melannotus* and *C. trifascialis* at Lizard Island (open bars) and One Tree Island (shaded bars) on the Great Barrier Reef (Australia). Bars represent (a) the mean coverage of 8 benthic categories counted in 10m line-intercept transects and (b) the mean number of individuals counted in $200m^2$ visual belt transects ± Standard Error (S.E). ANOVA results of significance of difference between locations for each species is indicated: *** = P < .001 ; ** = P < .01 ; * = P < .05 ; n.s. = not significant (P > .05). (#) symbols on *x*-axis labels indicate diet categories of hard corals. Dashed lines show the range of diet categories targeted by each of the four study species (*Chaetodon citrinellus, C. lunulatus*, *C. melannotus* and *C. trifascialis*).